
SPECIES LIMITS WITHIN THE *ARBORIMUS LONGICAUDUS* SPECIES-COMPLEX (MAMMALIA: RODENTIA) WITH A DESCRIPTION OF A NEW SPECIES FROM CALIFORNIA

MURRAY L. JOHNSON¹ AND SARAH B. GEORGE²

ABSTRACT. Karyotypic and morphologic variability was assessed in populations of red tree voles, *Arborimus longicaudus* species-complex, from Oregon and California. Diploid numbers vary from 52 in the north to 40 in the south. Populations from Oregon and California, separated by the Klamath Mountains, are strongly differentiated based on morphometric data, with individuals from southern populations smaller. Laboratory breeding studies demonstrated a reproductive barrier between northern and southern populations, and a new species is proposed for the red tree voles from California.

INTRODUCTION

The red tree vole, *Arborimus longicaudus* (True, 1890), formerly referred to *Phenacomys longicaudus* was described late in the sequence of taxonomic studies in North America. Frederick True (1890) provided the type description on the basis of a single specimen from Coos County, Oregon. A closely related species, *Arborimus* [*Phenacomys*] *silvicola* (Howell, 1921), described from Tillamook County, Oregon, has subsequently been classified as a subspecies of *A. longicaudus* (Johnson, 1968; Hall, 1981). Originally proposed as a subgenus of *Phenacomys*, *Arborimus* (Taylor, 1915) was elevated to generic rank by Johnson (1973); included within it are the red tree vole and the white-footed vole, *A. albipes* (Johnson and Maser, 1982).

The range of *A. longicaudus* was thought to extend from northwestern Oregon, south along the Pacific coast to Sonoma County, California (Benson and Borrell, 1931; Hall, 1981; Fig. 1). Coastal Oregon populations (*A. l. silvicola*) are characterized by their larger size and darker color than populations of *A. l. longicaudus* to the south and east. Johnson (1973) suggested that the California populations of the red tree vole represent an undescribed sibling species. Laboratory breeding studies, karyotypic analyses, and morphometric analyses were conducted to examine the systematic relationships among populations within this species complex. We report here the results of those investigations, update the taxonomy of the species

group, and describe the previously unrecognized sibling species in California.

MATERIALS AND METHODS

CHROMOSOMAL ANALYSES

Nineteen wild-caught and four captive Oregon $\times$ California cross individuals were karyotyped using the procedures of Hsu and Patton (1969) and Lee and Elder (1980). Karyotypes from two Oregon individuals were published by Hsu and Benirschke (1974). Collecting localities are listed in Table 1. Negatives are deposited in the laboratory of Dr. T.C. Hsu at M.D. Anderson Hospital in Houston, Texas (TCH). Voucher specimens are deposited in the collections of mammals at the University of Puget Sound, Tacoma, Washington (PSM), the Thomas Burke Memorial Washington State Museum, Seattle (UW), and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); TCH specimens are not cataloged (Table 1).

CAPTIVE BREEDING STUDIES

From 1955 to 1986, red tree voles were maintained in captivity. Cages were made of Douglas fir (*Pseudotsuga menziesii*) plywood and had plexiglas fronts and tops of vinyl-coated, half-inch screen. Three sizes were used: 60 cm deep $\times$ 20 cm wide $\times$ 38 cm high, 60 cm deep $\times$ 38 cm wide $\times$ 20 cm high, and for breeding, 60 cm deep $\times$ 114 cm wide $\times$ 40 cm high. Cage floors were covered with coarse Douglas fir sawdust. A cedar nest box with two openings and a removable top was provided in each unit; usually two nest boxes were kept in the breeding cages. An excess of Douglas fir terminal branches was kept in an earthenware bowl in each cage at all times; the bowl also provided water to the mice at all times.

Based on the report of Hamilton (1962), a more intensive breeding program was begun in 1965. Breeding encounters were arranged by placing an adult male with an adult female in a cage for 30 hours. In some cases, males and females were left in cages for up to 10 days. There was no significant difference between results of encounters that lasted less than 30 hours and those lasting

1. Thomas Burke Memorial Washington State Museum, DB-10, University of Washington, Seattle, Washington 98195.

2. Section of Mammalogy, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

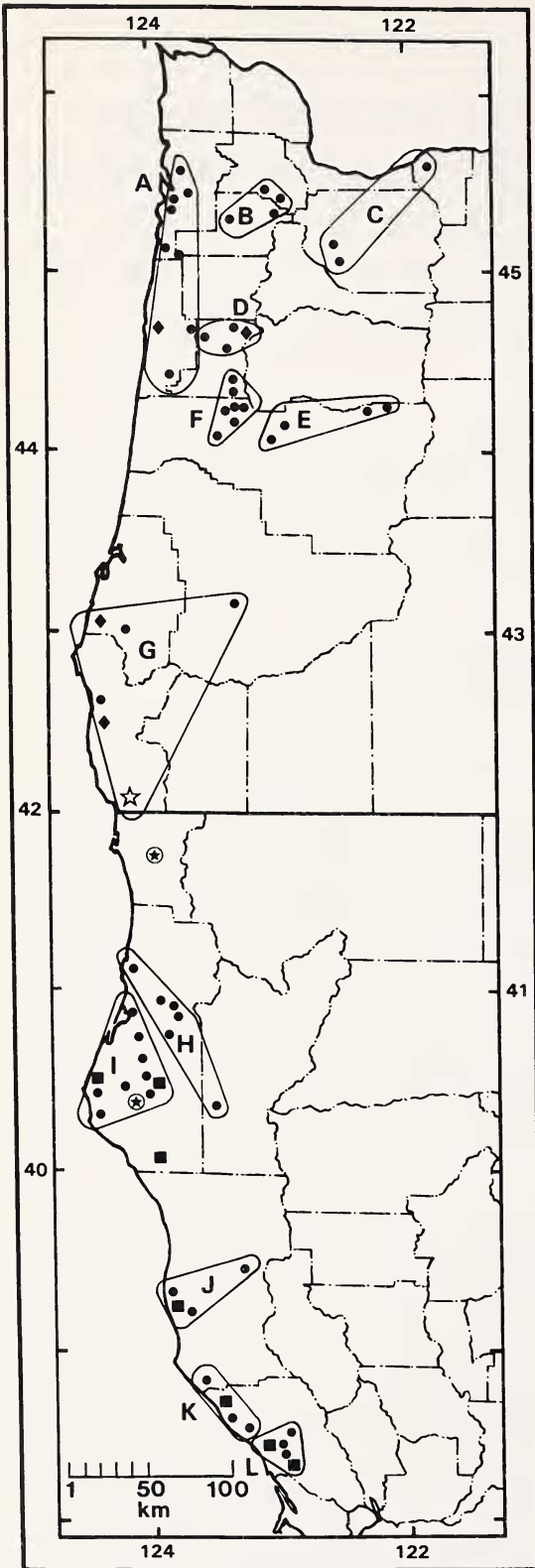


Figure 1. Locations of specimens in Oregon and California used in morphometric analyses are noted by dots. Diamonds denote karyotyped specimens with 2N = 52; open star denotes specimen with 2N = 48; stars enclosed

between 30 hours and 10 days (G-test, $P > 0.10$), therefore all results were considered together. This time was chosen as a reasonable biological period that a free-ranging male might court a receptive female in the wild. This optimized the chance of success with minimal risk to the males, which we observed to suffer a significant time-related mortality rate when caged with adult females (i.e., male mortality rose after 10 days with females).

Males and females were classified as being of Oregon (O) or California (C) origin; control encounters consisted of O $\times$ O and C $\times$ C arrangements, whereas test encounters consisted of O $\times$ C and C $\times$ O encounters. Based on the localities from which the animals were taken, it is assumed that the Oregon animals (with the exception of those from the Winchuk River area) had 2N = 52 and the California animals had 2N = 40. There may have been a California animal with 2N = 42, as not all individuals were karyotyped. There was no significant difference between results of encounters in which an individual from the Winchuk River area participated (G-test, $P > 0.10$), and therefore all encounters (including animals from the Winchuk River area) were combined.

Results of encounters were classified as negative (no known pregnancy), successful (production of litter surviving beyond 1 week), or as a pregnancy-related death (PRD). The latter category included maternal deaths (occurring during pregnancy or shortly after parturition), fetal deaths (aborted fetus(es) found in cage; abortion of fetuses early in pregnancy and resorption of fetuses are likely to be occult in occurrence, thus our estimates are probably low), and perinatal deaths (newborn litter dying in the arbitrarily set period of 1 week after parturition). Results were analyzed with an R $\times$ C test of independence using the G-test (Sokal and Rohlf, 1969) to determine if the number of successful pregnancies and PRDs were independent of the type of parental cross.

MORPHOMETRIC ANALYSES

A total of 306 adult specimens was examined from California and Oregon. These specimens are deposited in the collections listed in the acknowledgments. Specimens were aged on the basis of toothwear. An individual was classified as a juvenile if the reentrant angles of the molars were not evident above the alveolus, as an adult if molar roots were evident above the alveolus, and as an old adult if wear had obliterated the enamel pattern on the molar faces (Johnson, 1973). Juveniles and old adults were excluded. Three external measurements were recorded from specimen tags: head and body length (HB), tail length (TL), and hind foot length (HF). Five cranial measurements were taken using dial calipers, accurate to 0.1 mm: greatest length of skull (GLS), zygomatic breadth (ZB), least interorbital width (IOC), mastoid breadth (MB), and depth of braincase (DB). Nine cranial measurements were taken using an ocular micrometer, accurate to 0.1 mm: length of nasals (LN), length of maxillary tooththrow (MT), distance from the posteriormost point of nasals to posteriormost point of maxillaries (PW), width of interparietal (IPW), length of interparietal (IPL), M2-M2 width (MW), length of diastema (LD), width of upper M2 (TW), and length of palatal foramen (PF).

in circles denote specimens with 2N = 42; squares denote specimens with 2N = 40. Enclosures denote localities lumped for statistical purposes; letters refer to samples listed in the appendix.

Table 1. Collecting locality, sex, and diploid number of 23 specimens of *Arborimus* karyotyped. In the case of the hybrid individuals, the collecting localities of the parents are listed with the female first.

Locality	Voucher catalog no.	Sex	2N
OR: Benton Co.; McDonald Forest	PSM 10916	F	52
OR: Benton Co./Lane Co. line	PSM 10915	M	52
OR: Coos Co.; 2 mi. (3.2 km) W Bandon, Bill's Peak	PSM 10920	M	52
OR: Curry Co.; 1 mi. (1.6 km) S Humbug Mt.	PSM 23922	M	52
OR: Lincoln Co.; no specific locality	PSM 23928	F	52
OR: Curry Co.; Winchuk River	TCH 2447	F	48
CA: Del Norte Co.; S Fork Smith River, Big Flat	PSM 24934	M	42
CA: Humboldt Co.; 2 mi. (3.2 km) W Bridgeville	TCH 2448	M	42
CA: Humboldt Co.; 4.3 mi. (6.9 km) N Bridgeville	MVZ 140633	F	40
CA: Humboldt Co.; 3 mi. (4.8 km) N Capetown	MVZ 140517	M	40
CA: Humboldt Co.; 5 mi. (8 km) S Garberville	PSM 20937	M	40
CA: Mendocino Co.; Albion	PSM 20943	M	40
CA: Sonoma Co.; 1 mi. (1.6 km) E Stewart's Point	PSM 10943	M	40
CA: Sonoma Co.; Jenner	PSM 21019	F	40
CA: Sonoma Co.; Jenner	PSM 24040	F	40
CA: Sonoma Co.; Jenner	PSM 21017	M	40
CA: Sonoma Co.; Jenner	PSM 21024	M	40
CA: Sonoma Co.; Jenner	UW 34476	F	40
CA: Sonoma Co.; Freestone	PSM 21260	M	40
OR: Lane Co.; 6 mi. (9.7 km) NNE Coburg × CA: Mendocino Co.; Albion	PSM 24008	F	46
OR: Lane Co.; 6 mi. (9.7 km) NNE Coburg × CA: Mendocino Co.; Albion	PSM 24009	M	46
OR: Benton Co.; Monroe × CA: Mendocino Co.; Albion	PSM 24010	M	46

Standard statistics (mean, standard deviation, standard error, and coefficient of variation) were calculated for sample measurements using STATS of SYSTAT (1985). Twelve samples were pooled on the basis of subspecific classification and geographic locality (Fig. 1; see Specimens Examined in the appendix for sample sizes and specific localities). The four largest samples (A, F, I, and L; Fig. 1) were selected to test for significant differences between sexes using Student's *t*-test (SYSTAT, 1985). Females averaged larger in most cases, and for each sample, at least three measurements were significantly different between the sexes. Subsequently, males and females were analyzed separately. Far fewer males than females were available for study, and it was necessary to further pool male geographic samples. Thus male sample B includes samples B, D, and F; C includes C and E; and H includes H and I; J includes J, K, and L.

Tests of normality, Student-Newman-Keuls multiple range tests, and a one-way analysis of variance (*F*-test) for significant differences among means were done using BIOSTAT II (Pimentel and Smith, 1986). Multivariate analyses of variance (MANOVAs) and canonical analysis were used to assess the extent of morphometric divergence among samples. These were performed using PROC GLM of SAS for the MANOVAs (SAS Institute, 1985) and BIOSTAT II for the discriminant analysis (Pimentel and Smith, 1986).

RESULTS
CHROMOSOMAL ANALYSES

Four diploid numbers were documented in wild-caught individuals: 52, 48, 42, and 40 (Table 1). Northern specimens were characterized by a diploid number of 52 (Table 1; Fig. 1; Hsu and Be-

nirschke, 1974; with reexamination by V.R. Rausch, personal communication), with 22 pairs of acrocentric or subtelocentric autosomes, three pairs of small submetacentric autosomes, a large submetacentric X chromosome, and a small submetacentric Y chromosome. Southern individuals have a diploid number of 40 (Table 1, Figs. 1 and 2A), 5 pairs of large metacentric autosomes, 1 pair of large submetacentric autosomes, 11 pairs of small acrocentric or subtelocentric autosomes, 2 pairs of small submetacentric autosomes, and a small subtelocentric Y chromosome (not figured) and two morphologically distinct X chromosomes. One is a large submetacentric, similar in size and shape to that of northern population, the other is a large subtelocentric (Fig. 2). The 2N = 48 individual has a chromosomal morphology similar to the 2N = 52 individuals except that the former has four fewer acrocentric pairs and two additional pairs of large metacentric autosomes. The X chromosome is a large submetacentric. Specimens possessing 2N = 42 differ from the 2N = 40 individuals in having one less pair of large metacentric autosomes and two additional pairs of acrocentric or subtelocentric autosomes. All X chromosomes in these specimens are large telocentrics.

The F₁ hybrid individuals have 46 chromosomes (Fig. 2B). As would be predicted from the morphology of the parental karyotypes (Hsu, *in litt.*), there are 6 large metacentrics, 1 large submetacentric (which is probably the X chromosome from its northern mother), 35 acrocentric or subtelocentric

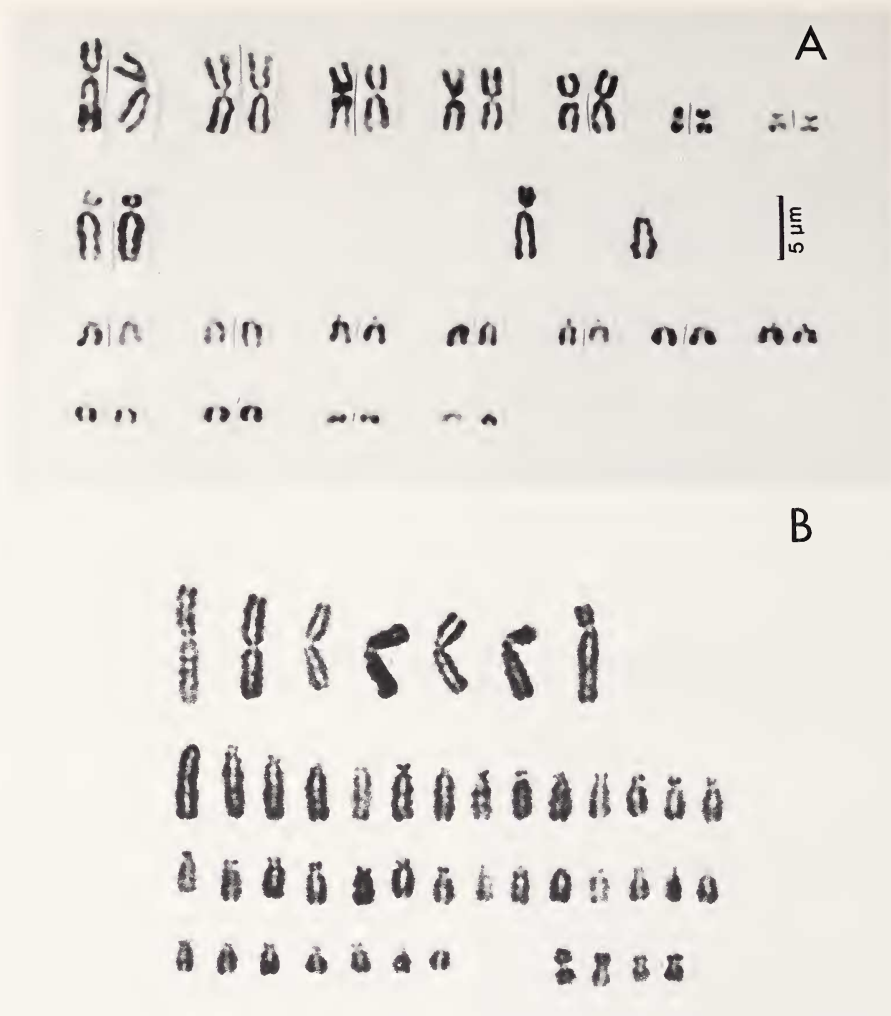


Figure 2. A. Karyotype of the holotype of *Arborimus pomo* n. sp., with 2N = 40, from Jenner, Sonoma Co., California. B. Karyotype of a male F₁ hybrid, provided by T.C. Hsu. The mother was from 6 mi. (9.7 km) NNE Coburg, Lane Co., Oregon, and the father was from Albion, Mendocino Co., California.

chromosomes (one of which is probably the Y chromosome from its southern father), and 4 small metacentric or submetacentric chromosomes.

CAPTIVE BREEDING STUDIES

Of 250 encounters recorded, 27 were Oregon × California crosses (Table 2). The G-value is 206.0, which is significant ($df = 6$; $\chi^2 = 18.6$), suggesting that results of encounters are not independent of the type of parental cross. The successful pregnancy rate for all Oregon–California crosses was 23%, slightly lower than that for the average of the within-state crosses (28%). The success of crosses between California females and Oregon males was strikingly lower than the reciprocal cross, suggesting a directional barrier to reproduction between northern and southern populations. When Oregon

and California individuals were crossed, the number of PRDs was much higher than for within-state crosses (17% vs. 3%), further indicating a barrier to reproduction between northern and southern populations.

MORPHOMETRIC ANALYSES

All F-values were significant ($P < 0.05$; Table 3). Oregon samples of both sexes averaged larger than California samples for variables HB, TL, HF, GLS, ZB, MT, LD, and TW for both sexes (Table 3). Variable IOC measured larger in Oregon males than California males, but the same was not true for females. For variable IPW, sample G individuals were as small as the California samples. Only for variable PW were California individuals larger than Oregon individuals.

Table 2. Results of breeding experiments. C denotes a California origin; O denotes an Oregon origin; PRD indicates pregnancy-related deaths. Proportions are in parentheses.

f × m	Negative	Successful	PRD	Total encounters
O × O	83 (0.66)	39 (0.31)	4 (0.03)	126 (1.00)
C × C	69 (0.73)	22 (0.23)	3 (0.03)	94 (1.00)
O × C	6 (0.46)	5 (0.38)	2 (0.15)	13 (1.00)
C × O	12 (0.70)	2 (0.12)	3 (0.18)	17 (1.00)
Total	160	61	12	250 (1.00)

The results of the Student–Newman–Keuls multiple range test (Table 3) indicate that there are few significant subgroups of samples. The exceptions are all in the male samples as follows: samples A and G are significantly larger for HF; California males are significantly larger than Oregon males for PW; sample J is significantly larger for PF; sample H is significantly smaller for LD; and for MT, males break in three significant subgroups (H/J, B/G/C, and H).

Results of the MANOVAs (Wilks’ criterion, Pillai’s trace, Hotelling–Lawley trace, and Roy’s maximum root criterion) were significant ($P < 0.0001$; upper bound for Roy’s) for both males and females. The canonical vectors expressed the following percentages of the morphometric variation (female/male): first—73.60/76.84; second—8.36/9.28; third—5.88/8.38. The first three canonical vectors are listed in Table 4. Characters with percentages of their variance over 80% explained by the first vector in females are HB, GLS, ZB, MB, LN, DB, PW, IPL, LD, and PF, whereas for males they are GLS, MT, DB, PW, IPL, LD, and PF. On the second vector, no characters had more than 50% of their variance explained for females, whereas for males, TL, HF, and ZB had more than 50% variance explained.

Two-dimensional plots of the first two canonical vectors for females and males (showing the sample mean and 95% confidence limits; Pimentel and Smith, 1986) are illustrated in Figure 3. The third vector is not illustrated as it accounts for a relatively small portion of the variability. For both sexes, Oregon samples (A–G) are separated from California samples (H–L) along the first vector. There appears to be some geographic pattern of alignment along the second vector within the cluster of Oregon populations. For example, for females, the samples align from A (the northernmost sample) to G (the southernmost sample in the left of Figure 3A, whereas the male populations do not fall out in any discernable geographic pattern. The same is seen in the clusters of male samples (Fig. 3B).

The degree of phenetic overlap of the samples was assessed further by comparing the proportion of individuals from each locality that were misclassified by the discriminant function analysis (Table 5). Of 306 individuals, 234 (76.5%) were classified correctly to their *a priori* designated samples by the discriminant function; 72 (23.4%) were clas-

sified incorrectly. Of the latter, only three (1.0%) were classified to populations in the other state (i.e., two California individuals misclassified to an Oregon sample, and one Oregon individual misclassified to a California sample). The remainder were misclassified to a within-state population.

DISCUSSION

Chromosomal analyses suggest that there are two distinct groups within specimens previously recognized as *A. longicaudus*. The northern (Oregon) group is typified by $2N = 52$, and a single type of X chromosome (a large submetacentric); the southern (California) group has a $2N$ of 40 or 42 and two types of X chromosomes. The differences in morphology between the two X chromosomes may be due to heterochromatic additions or losses. This variability is commonly seen in arvicolid voles (Modi, 1987), but its existence in *Arborimus* cannot be substantiated without C-banded karyotypes. The autosomal variability may be due to Robertsonian fission–fusion events. However, banded chromosomes and larger sample sizes are needed to test this hypothesis.

Morphometric results reflect a similar pattern distinguishing Oregon and California groups. Although the univariate statistics do not demonstrate easily discernable differences between the groups, Oregon individuals tend to be larger than California individuals. Also, the maxillaries in California individuals tend to project more posteriorly relative to the nasals than do the maxillaries in Oregon individuals. The multivariate results provide incontrovertible patterns of distinctness of the two groups. Laboratory breeding studies are concordant with the karyologic and morphologic results and demonstrate a strong reproductive barrier between Oregon and California populations.

Additional data on morphologic distinction between the two groups may be found in Kesner (1986). In an examination of the myology of the microtine manus, he demonstrated that individuals from California populations (referred to as *A. longicaudus*) possess a muscle (*M. adductor digiti secundi*) that is absent in individuals from northern populations (referred to as *A. silvicola*). In addition, California specimens possess the full complement of *Mm. lumbricales*, whereas Oregon specimens do not.

Table 3. Variation in 17 measurements (mm) for populations of *Arborimus*. Population samples and measurements are explained in the materials and methods section. Vertical lines alongside each geographic sample indicate statistically homogeneous subsets derived from a Student-Newman-Keuls multiple range test. All *F*-tests are highly significant ($P < 0.001$), except depth of braincase ($P < 0.05$ for both sexes), and tail length ($P < 0.05$ for males).

Sample	Mean	S.D.	Sample	Mean	S.D.
Head and body length (HB)					
Females ($F = 7.32$)			Males ($F = 6.38$)		
C	112.56	3.94	A	105.11	5.00
A	112.23	4.67	C	104.44	5.70
G	107.00	6.30	G	102.14	6.83
B	107.00	2.31	B	98.38	2.67
E	106.25	3.30	J	98.11	6.38
D	106.17	5.81	H	94.58	7.75
F	103.58	5.27			
I	103.29	7.30			
K	102.90	5.26			
H	102.60	6.13			
L	102.46	5.66			
J	101.50	6.95			
Tail length (TL)					
Females ($F = 4.12$)			Males ($F = 2.80$)		
E	79.25	9.32	G	71.14	5.87
D	79.00	5.44	B	70.75	4.93
C	78.89	5.35	C	70.00	4.18
B	75.43	7.37	J	68.27	5.92
A	75.23	5.44	A	66.89	5.31
G	74.75	5.31	H	64.17	5.22
F	74.21	6.55			
L	73.26	6.73			
H	70.80	8.23			
I	68.95	9.32			
J	68.17	7.52			
K	65.90	9.28			
Hind foot length (HF)					
Females ($F = 15.19$)			Males ($F = 14.80$)		
C	22.78	0.83	A	21.72	1.13
A	22.19	0.75	C	21.56	0.88
B	22.00	1.41	G	20.57	0.79
E	21.50	1.00	B	20.44	1.09
G	21.00	0.76	J	19.95	0.81
F	20.95	1.87	H	19.42	0.90
D	20.83	1.17			
L	20.18	0.83			
K	19.90	0.88			
I	19.57	1.33			
H	19.40	1.43			
J	19.33	0.52			
Greatest length of skull (GLS)					
Females ($F = 8.40$)			Males ($F = 13.07$)		
A	26.08	0.71	A	25.38	0.58
C	25.81	0.71	G	24.89	0.37
B	25.36	0.53	C	24.69	0.69
E	25.30	0.80	B	24.42	0.57
D	25.28	0.61	J	24.15	0.60
F	24.99	0.80	H	24.03	0.66
J	24.92	0.84			
G	24.81	0.62			
I	24.70	0.93			
L	24.54	0.72			
H	24.49	0.89			
K	24.49	0.98			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
Zygomatic breadth (ZB)					
Females ($F = 6.63$)			Males ($F = 8.66$)		
C	14.72	0.30	G	14.50	0.34
A	14.55	0.48	A	14.20	0.41
E	14.40	0.40	C	13.96	0.41
B	14.36	0.49	B	13.80	0.40
D	14.28	0.29	J	13.70	0.36
J	14.18	0.53	H	13.63	0.50
G	14.13	0.37			
F	14.11	0.43			
H	14.10	0.59			
I	14.03	0.59			
L	14.02	0.39			
K	13.99	0.25			
Least interorbital width (IOC)					
Females ($F = 6.81$)			Males ($F = 5.74$)		
B	3.59	0.20	A	3.48	0.13
H	3.47	0.18	C	3.44	0.14
A	3.46	0.10	B	3.44	0.19
C	3.41	0.13	G	3.37	0.21
K	3.34	0.18	H	3.33	0.22
D	3.32	0.18	J	3.28	0.14
G	3.31	0.21			
I	3.31	0.14			
L	3.27	0.14			
F	3.27	0.21			
E	3.22	0.17			
J	3.12	0.18			
Mastoid breadth (MB)					
Females ($F = 8.28$)			Males ($F = 4.66$)		
C	8.86	0.21	J	8.69	0.30
E	8.77	0.54	C	8.64	0.26
L	8.77	0.30	A	8.63	0.21
A	8.71	0.20	G	8.57	0.24
G	8.70	0.36	B	8.43	0.18
J	8.68	0.54	H	8.36	0.25
B	8.63	0.38			
K	8.62	0.25			
I	8.57	0.32			
D	8.53	0.21			
H	8.50	0.44			
F	8.47	0.45			
Length of nasals (LN)					
Females ($F = 5.59$)			Males ($F = 4.96$)		
A	6.85	0.35	G	6.84	0.31
C	6.82	0.33	A	6.61	0.27
I	6.72	0.46	H	6.43	0.52
G	6.68	0.50	C	6.32	0.36
H	6.67	0.39	J	6.29	0.38
E	6.65	0.31	B	6.26	0.19
J	6.58	0.31			
D	6.53	0.24			
K	6.51	0.44			
F	6.51	0.25			
B	6.50	0.33			
L	6.42	0.38			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
Length of maxillary tooththrow (MT)					
Females (F = 18.40)			Males (F = 20.40)		
A	5.90	0.16	A	5.86	0.16
C	5.77	0.18	C	5.70	0.19
B	5.76	0.15	G	5.63	0.13
E	5.75	0.29	B	5.56	0.17
D	5.58	0.23	J	5.43	0.17
G	5.55	0.19	H	5.41	0.17
F	5.50	0.23			
K	5.49	0.17			
L	5.47	0.19			
I	5.46	0.27			
J	5.45	0.19			
H	5.33	0.20			
Depth of braincase (DB)					
Females (F = 1.98)			Males (F = 2.84)		
H	7.26	0.37	J	7.19	0.29
J	7.23	0.52	A	7.16	0.20
A	7.23	0.20	G	7.11	0.21
L	7.23	0.29	H	7.08	0.24
B	7.20	0.08	C	7.01	0.27
I	7.16	0.28	B	6.93	0.25
F	7.15	0.32			
K	7.13	0.28			
E	7.12	0.17			
D	7.12	0.20			
G	7.03	0.23			
C	7.02	0.28			
Nasal-maxillary distance (PW)					
Females (F = 19.58)			Males (F = 8.28)		
I	1.11	0.25	J	0.89	0.30
L	0.99	0.24	H	0.86	0.33
J	0.98	0.17	B	0.56	0.26
H	0.89	0.35	A	0.56	0.28
K	0.82	0.11	C	0.53	0.15
B	0.66	0.22	G	0.44	0.19
D	0.58	0.15			
F	0.57	0.19			
A	0.53	0.17			
C	0.44	0.18			
E	0.35	0.17			
G	0.30	0.40			
Width of interparietal (IPW)					
Females (F = 15.36)			Males (F = 5.59)		
C	9.02	0.24	A	8.64	0.29
A	8.86	0.31	B	8.43	0.30
D	8.60	0.27	C	8.32	0.37
B	8.54	0.30	H	8.31	0.30
F	8.54	0.24	G	8.17	0.72
I	8.44	0.34	J	8.14	0.35
E	8.40	0.52			
H	8.37	0.35			
J	8.37	0.30			
K	8.27	0.50			
L	8.15	0.35			
G	7.83	0.37			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
Length of interparietal (IPL)					
Females (F = 7.71)			Males (F = 6.20)		
C	3.72	0.25	J	3.54	0.31
K	3.72	0.40	C	3.40	0.24
L	3.68	0.28	H	3.31	0.30
H	3.62	0.50	B	3.27	0.26
E	3.58	0.13	G	3.24	0.36
I	3.55	0.31	A	3.16	0.19
J	3.52	0.41			
F	3.33	0.25			
G	3.29	0.23			
B	3.27	0.24			
A	3.21	0.25			
D	3.20	0.30			
M2-M2 width (MW)					
Females (F = 15.47)			Males (F = 12.50)		
C	5.84	0.17	A	5.78	0.16
A	5.84	0.19	C	5.69	0.17
E	5.70	0.08	G	5.54	0.24
B	5.64	0.19	H	5.52	0.19
D	5.60	0.20	B	5.49	0.20
J	5.53	0.21	J	5.39	0.19
G	5.47	0.16			
H	5.46	0.18			
I	5.46	0.18			
F	5.41	0.23			
L	5.40	0.18			
K	5.38	0.14			
Length of diastema (LD)					
Females (F = 8.56)			Males (F = 13.91)		
C	7.54	0.43	A	7.14	0.20
A	7.45	0.33	C	7.02	0.19
B	7.17	0.21	G	6.84	0.24
E	7.10	0.26	B	6.84	0.21
F	6.98	0.35	J	6.76	0.28
D	6.98	0.22	H	6.45	0.22
G	6.90	0.33			
L	6.83	0.36			
K	6.82	0.46			
J	6.82	0.48			
H	6.71	0.43			
I	6.67	0.37			
Width of upper M2 (TW)					
Females (F = 9.89)			Males (F = 8.26)		
E	1.35	0.06	C	1.31	0.08
C	1.33	0.07	A	1.31	0.07
A	1.31	0.05	B	1.26	0.05
D	1.30	0.06	G	1.23	0.08
F	1.25	0.06	H	1.23	0.06
B	1.24	0.05	J	1.22	0.06
J	1.23	0.08			
L	1.22	0.06			
K	1.22	0.08			
G	1.21	0.04			
I	1.20	0.05			
H	1.20	0.05			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
Length of palatal foramen (PF)					
Females (F = 7.15)			Males (F = 17.85)		
L	4.71	0.23	J	4.61	0.19
A	4.69	0.18	A	4.50	0.11
J	4.68	0.26	H	4.40	0.14
I	4.59	0.22	C	4.33	0.19
K	4.58	0.29	G	4.31	0.14
C	4.56	0.22	B	4.18	0.20
B	4.51	0.11			
H	4.47	0.24			
D	4.45	0.26			
E	4.40	0.18			
F	4.27	0.26			
G	4.24	0.42			

The tree voles obtained from Curry County, Oregon (2N = 48), and Del Norte County, California (2N = 42) represent new locality records located in a long-recognized hiatus in the distribution of "*Arborimus longicaudus*." Each was from a very small isolated and restricted population. When these populations were last monitored in 1985, evidence of persistence was poor, restricted to several inaccessible (to us) nests. These individuals do not represent either F₁ or F₂ hybrids (Fig. 2B; T.C. Hsu, personal communication). Based upon the morphology of the X chromosome and the results of the morphometric analyses, the affinity of the population represented by the 2N = 48 individual is

with other Oregon samples, whereas the affinities of the populations represented by the 2N = 42 individuals is with other California samples.

One may argue that the morphological gap between the Oregon and California samples (Fig. 3) reflects nothing more than a lack of specimens from that geographic area, and should specimens exist from that area, the gap would be filled in. We refute this argument by pointing out that within both Oregon and California there are geographic gaps not represented by any samples (e.g., between F and G, or between H/I and J) that are as large as or larger than the geographic gap between samples G and H (Fig. 1). Clustering of within-state samples (Fig. 3)

Table 4. First three canonical vectors and percent of overall morphometric variation explained by each vector for 17 variables in both females and males.

Variable	Females			Males		
	CV1	CV2	CV3	CV1	CV2	CV3
HB	-0.010	-0.004	-0.009	0.001	-0.001	-0.006
TL	-0.002	0.010	-0.004	0.001	0.016	-0.012
HF	-0.047	0.050	0.055	-0.020	-0.107	-0.028
GLS	-0.151	-0.143	-0.077	-0.169	-0.089	0.148
ZB	0.117	0.104	-0.042	0.073	0.416	-0.136
IOC	-0.028	-0.334	0.004	-0.091	0.145	-0.074
MB	0.304	0.217	0.107	0.155	-0.240	-0.219
LN	0.259	-0.235	-0.247	0.224	0.268	0.201
MT	-0.118	-0.084	0.204	-0.311	-0.072	-0.270
DB	0.196	0.038	0.060	0.078	-0.065	0.021
PW	0.514	-0.443	0.002	0.268	0.043	0.210
IPW	-0.164	-0.288	-0.052	-0.093	-0.085	0.206
IPL	0.206	0.097	0.093	0.244	0.011	-0.259
MW	-0.280	-0.333	0.127	-0.030	-0.218	0.658
LD	-0.251	0.197	0.229	-0.372	-0.159	-0.365
TW	-0.318	0.502	0.702	-0.351	-0.241	-0.181
PF	0.415	-0.231	0.547	0.615	-0.712	0.196
Percent	73.60	8.36	5.88	76.84	9.28	8.38

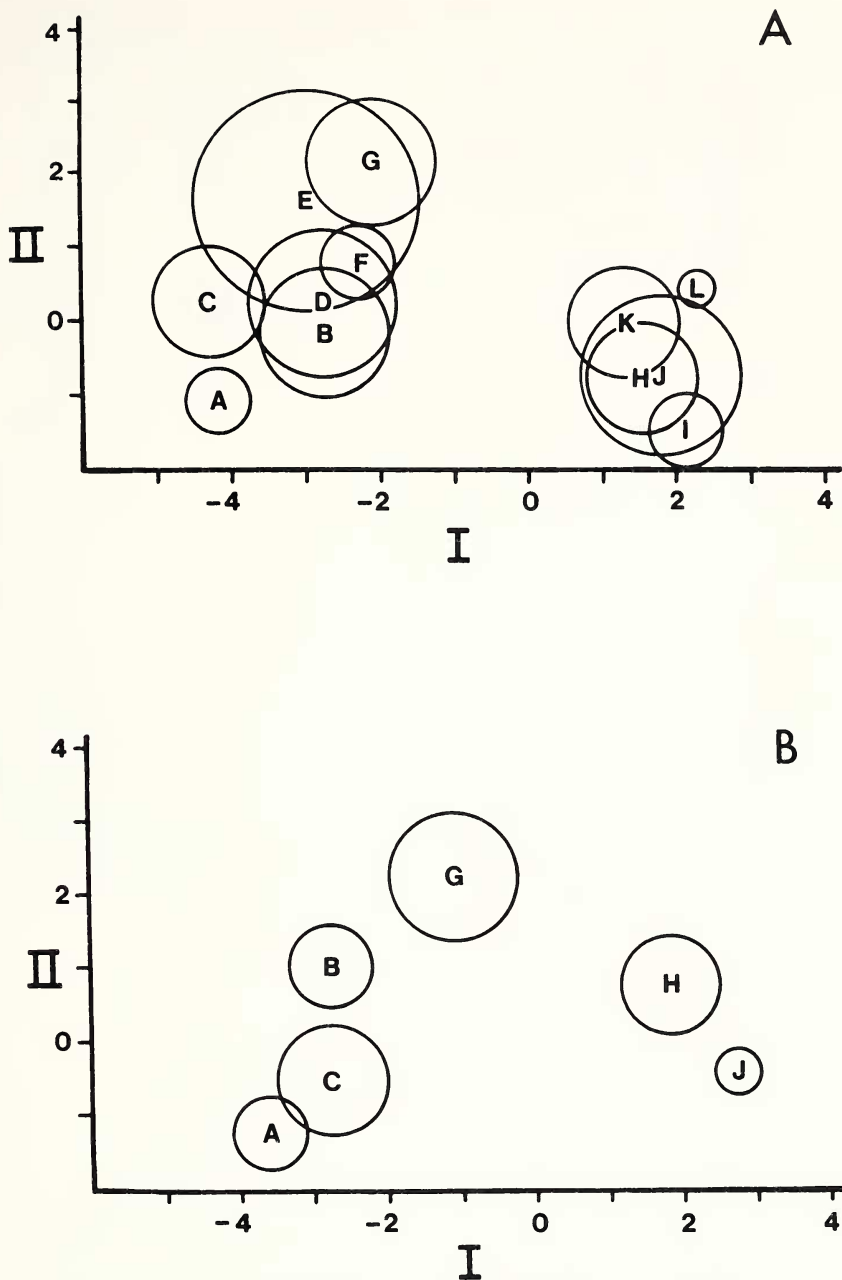


Figure 3. Plot of the mean and one standard deviation of the first two canonical variates for 12 samples of females (top) and six samples of males (bottom) belonging to the *Arborimus longicaudus* species-complex. Letters refer to samples identified in the appendix.

does not reflect these geographic gaps, further suggesting a genetic component to the gap between Oregon and California samples.

In light of the data presented here (Tables 1, 2, and 5; Figs. 1-3), we recognize the California populations as a distinct biological species. By Mayr's (1969) discrimination grid, the two species are grossly morphologically identical, are allopatric, and are reproductively isolated, therefore they may be con-

sidered sibling species. The name *A. longicaudus* in the broad sense (type locality, Marshfield, Coos County, Oregon) must be applied to the Oregon group, leaving the California species without an available name; it is described and named below.

The hiatus between the northern and southern species of red tree voles exists in the Klamath Mountains area. This region is significantly higher in altitude and geologically older than the Coast

Table 5. Geisser classification of individual red tree voles (n = 306). Rows are actual groups and columns are predicted groups. Asterisks indicate specimens classified to a sample outside of the state (see results section). See appendix for explanation of sample acronyms.

Actual group	n	Percent classified correctly	Predicted locality											
			A	B	C	D	E	F	G	H	I	J	K	L
A) Females														
A	26	92	24			2								
B	7	71		5		1		1						
C	9	89	1		8									
D	6	67			1	4		1						
E	4	50			1		2		1					
F	19	63		1	1	3	1	12				1*		
G	8	88				1			7					
H	10	50				1*				5	2	1		1
I	21	71								3	15	1	1	1
J	6	67										4	2	
K	9	70										1	7	2
L	74	70								2	4	5	11	74
B) Males														
A	18	89	16	1	1									
B	16	75	1	12	3									
C	8	56	3	1	5									
G	7	71		1					5					1*
H	12	92								11			1	
K	44	91								4				40

Ranges to the north and south, and is dissected by rivers running through narrow, steep-walled canyons (Bailey, 1966; Wright and Frey, 1965). The climate and vegetation of this region reflect the geology and geography, in that the area is more arid, with a rain shadow closer to the coast, and therefore has a more compressed mesic vegetation belt. The flora is diverse and rich in narrowly endemic species (Whittaker, 1961), lacking large continuous stands of Douglas fir and associates (*Tsuga heterophylla*, *Picea sitchensis*, *Abies grandis*, and *A. concolor*), which are primary food sources for red tree voles. Distributions of a number of species-complexes of animals reflect this fragmentation of the mesic forest (Maser et al., 1981; Nussbaum et al., 1983). An example is the *Eutamias townsendi* species-complex, where sibling species of chipmunks appear to be separated geographically by the Rogue, Klamath, and Eel rivers in the Klamath Mountains area (Levenson et al., 1985; Sutton, 1987). Isolation by the combination of these environmental factors may be an important factor in speciation within the *A. longicaudus* species-complex as well.

There is not any strong morphometric or karyologic differentiation between *A. l. longicaudus* and *A. l. silvicola* in Oregon. The two taxa have been distinguished primarily on the basis of color (Hall, 1981) but now can be properly delineated geographically. The darker race, *A. l. silvicola*, is restricted to the Pacific slope of the coast ranges in

Tillamook and Lincoln counties in Oregon (sample A in Fig. 1). The nominotypical subspecies is distributed to the east and south (samples B–G in Fig. 1).

Arboremus pomo new species

HOLOTYPE. Adult female, skin, skeleton, and karyotype, no. 34476, mammal collection, Thomas Burke Memorial Washington State Museum, University of Washington; from Jenner Ridge, 0.8 km (0.5 mi.) north of Jenner, Sonoma County, California (T7N, R11W, NW¼, Sec. 18; 38°27'30"N, 123°6'W). Taken on 24 February 1984 by M.L. and S. Johnson, sacrificed for karyotyping 13 March 1985, original number R. Rausch 46529. Skull is drawn in Figure 4.

PARATYPES. Several collections have series of specimens from the area of the type locality, including the Museum of Vertebrate Zoology, University of California at Berkeley; the University of Puget Sound; the Burke Museum, University of Washington.

DISTRIBUTION. All California populations formerly included within *A. longicaudus* (Fig. 1). The most southern record is from Freestone, Sonoma County, California. Specimens are available from scattered localities in Sonoma, Mendocino, Humboldt, and western Trinity counties. The northernmost population was collected from the South Fork of the Smith River, Del Norte County, California.

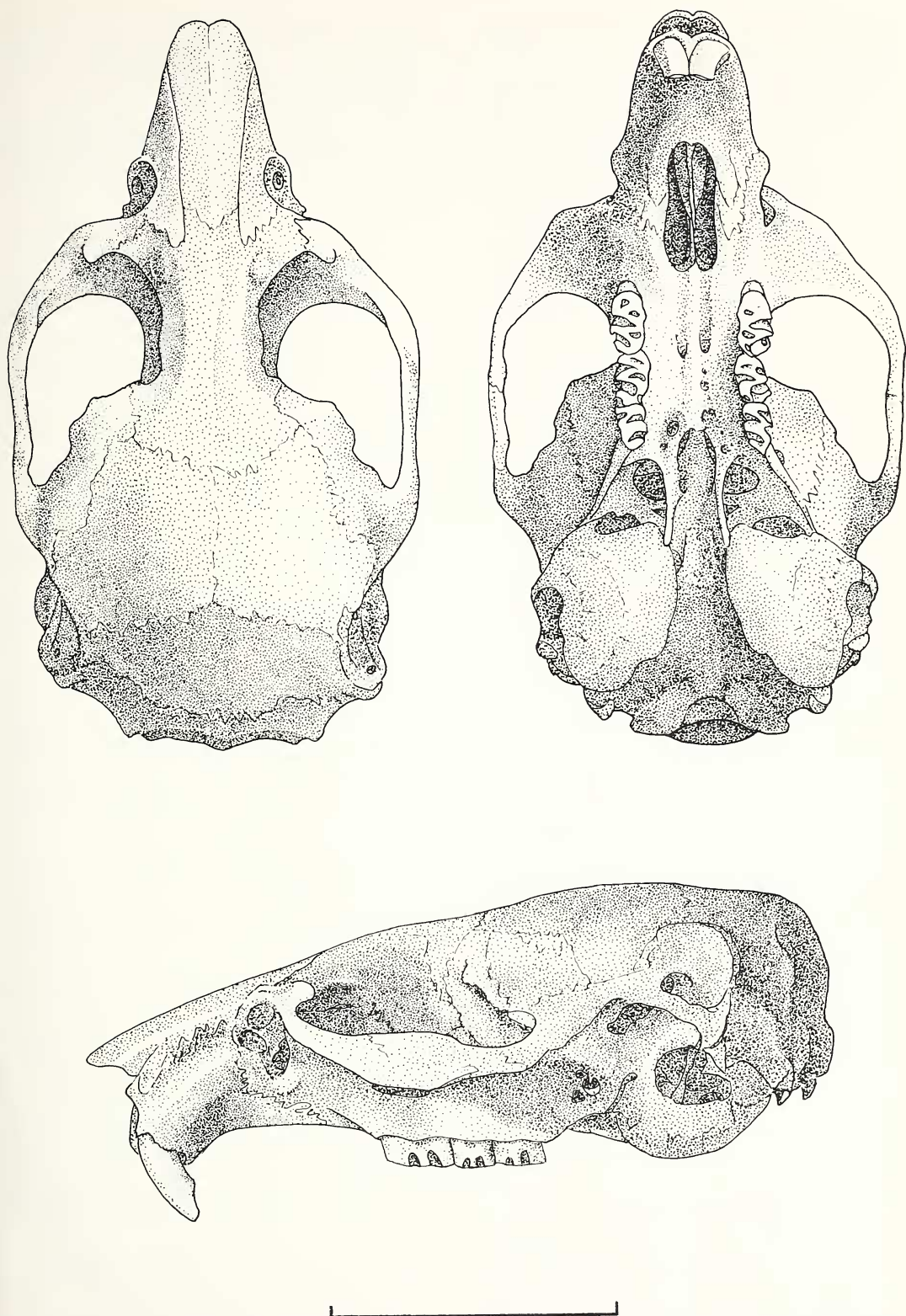


Figure 4. Dorsal, ventral, and side view of cranium of holotype of *Arborimus pomo* n. sp. (UW 34476). Bar is 1 cm.

DIAGNOSIS. *Arborimus pomo* has a diploid number of 40 or 42, with a large submetacentric and/or a large subtelocentric X chromosome, and a small subtelocentric Y chromosome. Specimens are smaller in overall size than those of *A. longicaudus*, the nasals do not extend as far posteriorly relative to the maxillaries as do the nasals in *A. longicaudus*, and specimens have a full set of *Mm. lumbricales* and *M. adductor digiti secundi*.

DESCRIPTION. *Arborimus pomo* is a true sibling species to *A. longicaudus*, the former being identical in coloration and external morphology to *Arborimus l. longicaudus* in southwestern Oregon. The color above is nearly uniform, bright rusty brown; the undersurfaces are white, slightly tinged with rusty brown, especially on the abdomen. The tail is dusky brown above, somewhat paler below. Measurements of the holotype (in mm) are: total length, 180; length of tail, 75; length of hind foot, 23; ear, 11.5; greatest length of skull, 25.9; zygomatic breadth, 14.5; least interorbital width, 3.4; mastoid breadth, 8.7; length of nasals, 6.9; length of maxillary toothrow, 5.4; depth of braincase, 7.2; distance from the posteriormost point of nasals to posteriormost point of maxillaries, 0.7; width of interparietal, 8.7; length of interparietal, 4.0; M2-M2 width, 5.3; length of diastema, 7.2; width of upper M2, 1.2; length of palatal foramen, 4.7.

ETYMOLOGY. The specific name refers to the Pomo peoples, indigenous to northern coastal California. The Pomo had a subsistence culture based on acorn processing and are widely respected for their basketry work. The name is a noun in apposition.

ECOLOGY. The habitat of *A. pomo* has been compared by repetitive monitoring and field studies to plant communities inhabited by *A. longicaudus* in Oregon (C. Maser and M.L. Johnson, *in litt.*). We can distinguish no particular pattern of difference. These mice inhabit a wide variety of mesic habitats, including those dominated by: (1) Douglas fir (*Pseudotsuga menziesii*), (2) grand fir (*A. grandis*), (3) Sitka spruce (*P. sitchensis*), or (4) western hemlock (*T. heterophylla*). Within the geographic range of these trees in northern California, those areas that have sufficient moisture (from ocean fog, increased precipitation, and permanent ground water such as along streams or around lakes) appear suitable for red tree voles. Habits of *A. pomo* were described in detail by Howell (1926; as "*Phenacomys longicaudus*").

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at Berkeley (MVZ); B.J. Verts, Department of Wildlife and Fisheries, Oregon State University (OSU); E. Kritzman, University of Puget Sound (PSM); R. Fisher, National Museum of Natural History (USNM).

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APPENDIX

Single letters in parentheses are sample designations used in morphometric analyses. Sample sizes are indicated by numbers following specific localities. Complete names for collections in which specimens are housed are given in the acknowledgments; LACM refers to specimens housed at the Natural History Museum of Los Angeles County.

Arborimus longicaudus silvicola

OREGON: (A; 26 females, 18 males) Lincoln Co.: near Grande Ronde (UW 34494, PSM 23928–9); near Nashville (FMNH 51496); Tillamook Co.: 3 mi. (4.8 km) E Cape Lookout, headwaters Tillamook River (PSM 21506, 21517, 21521, 22745–6); Cape Meares (PSM 22719); Cascade Head (PSM 21592); Foley Creek (UW 34487); Netarts (PSM 22723); ¾ mi. (1.2 km) SE Netarts Summit (UW 34490); approximately 1 mi. (1.6 km) SE Netarts Summit (UW 34493); Netarts Watershed, Crown Zellerbach Logging Area (PSM 21590, 21594–5, 21597–8); Oceanside (PSM 6781, 6784); Neskowin (MVZ 104979); 5 mi. (8 km) NW Pleasant Valley (PSM 21519–20); 3–4 mi. (4.8–6.4 km) E Tillamook, Bay Ocean Road (PSM 21515); 3 mi. (4.8 km) SW Tillamook, past Eckloft Road (PSM 21522); vicinity of Tillamook (UW 34484, PSM 21507, 21510–1, 21513); south Tillamook Bay (UW 34486, PSM 21553, 21587, 21709–10, 21712, 21715–7, 22716–8, 22720).

Arborimus longicaudus longicaudus

OREGON: (B; 7 females, 2 males) Washington Co.: 3 mi. (4.8 km) E Gaston (AMNH 175922); 5 mi. (8 km) E Gaston (AMNH 183335); 1½ mi. (2.4 km) SE Laurelwood (PSM 23926, 23970); Yamhill Co.: 9 mi. (14.5 km) W Carlton (MVZ 126859–60); 4 mi. (6.4 km) N Newburg, Ribbon Ridge (AMNH 183338, 183341, 183343).

(C; 9 females, 4 males) Clackamas Co.: Molalla (PSM 5871, 5873); 7½ mi. (12.1 km) SE Molalla (PSM 5870); 8 mi. (12.9 km) SE Molalla (PSM 10378, 10380, 10382, 10414, 23963, 23969); 8½ mi. (13.7 km) SE Molalla (PSM 8387); near Molalla, Schoenborn Ranch (PSM 5859, 10381); Hood River Co.: 1 mi. (1.6 km) E Cascade Locks, Oxbow Fish Hatchery (PSM 7019).

(D; 6 females, 5 males) Benton Co.: Alsea River, Seely Creek (PSM 23962); near Blodgett (FMNH 51495); 3¾ mi. (6 km) WNW Camp Adair (PSM 10400); 6 mi. (9.7 km) N Corvallis, Nettleton Road, McDonald Forest (OSU 5030, 5050, 5069); McDonald Forest (UW 34497, OSU 5048, 5075, PSM 10906); Prairie Mt., 3200 ft. (975 m) (T14S, R7W, SW¼, Sec. 7) (PSM 13107).

(E; 4 females, 5 males) Lane Co.: 6.8 km N, 7.6 km E Blue River (T15S, R5E, Sec. 32) (USNM 557648, 560412); 6 mi. (9.7 km) NNE Coburg (PSM 10441, 10927); 2½ mi. (4 km) SW Donna (PSM 10437); Eugene, Spencer Butte (OSU 5038); 6.4 km N, 0.6 km E McKenzie Bridge (T15S, R5E, Sec. 25) (USNM 558062); 6 km N, 0.6 km E McKenzie Bridge (T15S, R5E, Sec. 25) (USNM 557645); Linn Co.: 4½ mi. (7.2 km) S Sodaville (OSU 5079).

(F; 19 females, 9 males) Benton Co.: 5 mi. (8 km) S Alpine, Ferguson Creek (PSM 10404); NW Bellfountain (PSM 23904); 4 mi. (6.4 km) S Monroe (PSM 23906–7); 4.5 mi. (7.2 km) SW Monroe (OSU 5072, PSM 10383, 10389, 10399, 10406, 10409, 10411, 10917, 13104, 13109, 23892); Lane Co.: 6 mi. (9.7 km) NW Cheshire (PSM 10926); 6.75 mi. WNW Cheshire (OSU 5045); 3 mi. (4.8 km) W Cheshire (PSM 10433); 2¾ mi. (4.4 km) W Cheshire, near Jones Creek (OSU 5071); 5½ mi. (8.9 km) SW Cheshire (PSM 10436); 11 mi. (17.7 km) W Junction City (T5S, R5W, SE¼, Sec. 15) (PSM 23910, 23912, 23915); 6 mi. (9.7 km) SW Monroe (OSU 582, PSM 23913, 23916); 1½ mi. (2.4 km) NW Noti (PSM 10434); ¼ mi. (0.4 km) NE Waterville (PSM 10922).

(G; 8 females, 7 males) Coos Co.: 7 mi. (11.3 km) SW Bandon, Bill's Peak (PSM 23919–20); 1 mi. (1.6 km) NW Bill's Peak, 1200 ft. (366 m) (PSM 10920); 3 mi. (4.8 km) SW Broadbent (T30S, R13W, Sec. 12) (PSM 14498–9); Curry Co.: 1.1 mi. (1.8 km) SE Humbug Mt., along Hwy 101 (PSM 23924); Winchuk River at Wheeler Creek (PSM 23936–7, 23945, 23947, 23951–2, 23954, 23957–8).

Arborimus pomo

CALIFORNIA: (H; 10 females, 5 males) Humboldt Co.: 4 mi. (6.4 km) N, 11 mi. (17.7 km) E Arcata (PSM 20941); 8 mi. (12.9 km) E Blue Lake, Snow Camp Road (HSU 2338, 2370, 2372, 2376, 2378); Maple Creek, 1 mi. (1.6 km) N junction Mad River (MVZ 99616–8, 99621, 99624); Patrick Point State Park (PSM 10425, 20938); Trinity Co.: Mad River, South Fork Mountain, 2500 ft. (762 m) (MVZ 57039); Reilly's Ranch, South Fork Mountain, 3000 ft. (915 m) (MVZ 57042).

(I; 21 females, 7 males) Humboldt Co.: Arcata, Fickle Hill Road (HSU 3770); 5 mi. (8 km) E Arcata on Fickle Hill Road (CSULB 10497); Big Bend, Mad River (MVZ 19130); 8½ mi. (13.7 km) N Bridgeville (HSU 1410, 1427, 1612, 1614); 4.5 mi. (7.2 km) N Bridgeville (MVZ 140635); 4.3 mi. (6.9 km) N Bridgeville (MVZ 140633); 2 mi. (3.2 km) E Bridgeville (MVZ 47133); 5.3 mi. (8.5 km) NE Capetown, Morrow Ranch (MVZ 120595); Carlotta (MVZ 21148–54, USNM 206376, 206378–80, 206382–3); Cuddeback (MVZ 19174); 1.3 mi. (2 km) N Hydenville on Rohnerville Road (PSM 10423); 0.75 mi. (1.2 km) W Kneeland, New Kneeland Rd. (HSU 969); 1.5 mi. (2.4 km) S Kneeland, Old Kneeland Rd. (MVZ 165902).

(J; 6 females, 4 males) Mendocino Co.: 1½ mi. (2.4 km)

N Albion (AMNH 178883-7); Albion (PSM 10929); ¼ mi. (0.4 km) E Albion (PSM 10420, 10930); Mendocino City (MVZ 19973); 5 mi. (8 km) S Mt. Sanhedrin, Emandal Ranch (PSM 20945).

(K; 10 females, 4 males) Mendocino Co.: Anchor Bay (CM 16427); Sonoma Co.: 3 mi. (4.8 km) N Fort Ross (PSM 10934); 2.8 mi. (4.5 km) S Fort Ross (PSM 21088, 21101, 24036); 0.3 mi. (0.5 km) E Stewarts Point (PSM 10944); 0.4 mi. (0.6 km) E Stewarts Point (PSM 10942); ½ mi. (0.8 km) E Stewarts Point (MVZ 112394, PSM 21121); 1 mi. (1.6 km) E Stewarts Point (PSM 10940, 10943, 21098); 1¼ mi (2 km) E Stewarts Point (PSM 21481); 1 mi. (1.6 km) SSE Stewarts Point (MVZ 112424).

(L; 74 females, 36 males) Sonoma Co.: 1 mi. (1.6 km) N, 0.2 mi. (0.3 km) E Bridgehaven (MVZ 128791); 3.5 mi. (5.6 km) N Camp Meeker (MVZ 94759); 1 mi. (1.6 km) N Camp Meeker (PSM 21438-9, 21442, 21444-5); 3½ mi. (5.6 km) W Duncan Mills (MVZ 70189); 3 mi. (4.8 km) W Duncan Mills (MVZ 94760); 2 mi. (3.2 km) W Duncan Mills, Russian River (MVZ 94716, 94721); 3 mi. (4.8 km) E Duncan Mills (MVZ 70190); ½ mi. (0.8 km) SE Duncan Mills (PSM 21464); between Duncan Mills and Jenner (PSM 21167, 21256, 21258); near Duncan Mills, Rien's Beach (PSM 21491, 21496); ½ mi. (0.8 km) NW Freestone (PSM 21089-90, 21099-100, 21125, 21260); ½ mi. (0.8 km) N Freestone (PSM 21116, 21118-

9, 21168-70); Freestone (PSM 21263); 3 mi. (4.8 km) N Jenner, Willig Ranch (PSM 21406, 21408); 2 mi. (3.2 km) N Jenner, Willig Ranch (PSM 21399, 21401); ½ mi. (0.8 km) NW Jenner (PSM 21384, 21386, 21397-8); ½ mi. (0.8 km) N Jenner (PSM 21499); Jenner Ridge, 0.8 km (½ mi.) N Jenner (T7N, R11W, NW¼, Sec. 18) (UW 34458, 34462, 34476, LACM 85688-92, PSM 20970, 20973, 20976-8, 21016, 21019-20, 21025, 21028, 21412, 21415-6, 24037, 24040, 24048); 1 mi. (1.6 km) E Jenner (MVZ 103482, PSM 21349, 21352, 21354-62); 1.5 mi. (2.4 km) E Jenner (PSM 21347-48); 2 mi. (3.2 km) E Jenner (PSM 21363, 21365-6, 21368); Jenner area (PSM 21466); 1 mi. (1.6 km) W Monte Rio (CM 16426); 2 mi. (3.2 km) SE Monte Rio (CM 16425); 2.3 mi. (3.7 km) S Monte Rio (MVZ 70191, 70195, 70197); 3 mi. (4.8 km) S Monte Rio (PSM 21450, 21452, 21468); 4 mi. (6.4 km) S Monte Rio (MVZ 70201); 1 mi. (1.6 km) S Occidental (MVZ 94761); near Occidental, Camp Meeker (PSM 21426, 21429, 21432-4); Russian River (PSM 21172); lower Russian River, halfway between Duncan Mills and highway junction (PSM 21261-2, 21264); S side Russian River, ¼ mi. (0.4 km) upriver from Duncan Mills (PSM 21093, 21369, 21418, 21421); S side Russian River, ½ mi. (0.8 km) S Duncan Mills, Cassini Ranch (PSM 21376, 21379-80); ¼ mi. (0.4 km) W junction Sheephouse Creek and Russian River (MVZ 122096).